Phenotypic Stability of Resistance to Late Blight in Potato Clones Evaluated at Eight Sites in the United States

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ABSTRACT

Changes in the fungal pathogen *Phytophthora infestans* in the United States pose a significant threat to potato production. Sources of resistance to these new genotypes of *P. infestans* need to be identified for potato breeders to have parental materials for crossing, and the phenotypic stability of late blight resistance in these potato clones needs to be determined. Sixteen potato clones which reportedly have some resistance to late blight were evaluated at eight locations: Florida (FL), Maine (ME), Michigan (MI), Minnesota (MN), North Dakota (ND), New York (NY), Pennsylvania (PA) and Wisconsin (WI) in 1996. Percent infected foliage was recorded at approximately weekly intervals following the onset of the disease at each location. Area under the disease progress curve (AUDPC) was calculated. Clones were ranked for mean AUDPC within location and the nonparametric stability statistics, mean absolute rank differences and variance of the ranks, were analyzed for phenotypic stability. Neither of these statistics was significant, indicating a lack of genotype x environment interaction on the rankings of these clones across locations in 1996. The four clones with lowest AUDPC scores were U.S. clones AWN86514-2, B0692-4, B0718-3 and B0767-2. These clones should be useful parental materials for breeders seeking to incorporate genes for late blight resistance into potatoes.

INTRODUCTION

Potato late blight, caused by *Phytophthora infestans* (Mont.) de Bary, is the most devastating fungal disease of potatoes worldwide (Hooker, 1981). Resistance to late blight was known to occur in *Solanum demissum* Lindley (Müller and Black, 1952) and in *S. stoloniferum* Schldl. & Bouché (Schick *et al.*, 1958) and these species were utilized in potato breeding programs in the early twentieth century. Eleven major R genes have been reported in *S. demissum* (Black *et al.*, 1953; Malcolmson and Black, 1966). The resistance in *S. stoloniferum* and *S. demissum* is the same type (Schick *et al;* 1958). However, compatible fungal races for most R genes are now common, with the most complex *P. infestans* races in Mexico having all 11 known virulence factors (Rivera-Peña, 1990). Races with nine virulence factors have been reported in Europe (Schöber and Turkensteen, 1992). Goodwin *et al.* (1995) reported that three isolates of *P. infestans* clone US-8, presently the most widespread clone in the US, were pathogenic against the nine race-specific differentials used (R1, R2, R3, R4, R5, R7, R8, R9, R10).

Breeding for resistance to late blight became relatively unimportant in the United States after the middle of the twentieth century following the introduction of highly effective late blight fungicides, coupled with the failure of R genes to effectively control the disease. Many major potato producing areas of the United States developed late blight forecasting and spray recommendation programs, such as the model developed by Krause *et al.* (1975).

The central highlands of Mexico are the likely center of origin for *P. infestans* (Niederhauser, 1991). The Mexican isolates of *P. infestans* have greater genetic diversity for

virulence than isolates from anywhere else in the world (Tooley et al., 1986; Niederhauser et al., 1954). Prior to the 1980's, only the A1 mating type of P. infestans had been detected outside of central Mexico (Fry et al., 1993). However, probably due to migration from Mexico, the A2 mating type began to appear in Europe in the 1980's (Spielman et al., 1991) and subsequently spread to the United States and Canada (Deahl et al., 1991). These new isolates of P. infestans are more aggressive than the old isolates and have rapidly displaced the old isolates (Fry et al., 1993). In addition to being more aggressive, some of these new isolates are resistant to metalaxyl [N- (2,6-dimethylphenyl)-N- (methoxy-acetyl)-alanine methyl ester] (Deahl et al., 1992), the only systemic fungicide previously applied for control. It has been found that metalaxyl may actually be beneficial to some metalaxyl-resistant isolates of P. infestans (Zhang et al., 1997). The ability of the fungus to evolve and adapt has necessitated a more intense breeding effort to develop late blight resistant cultivars to replace the cultivars currently grown, which are not resistant.

Field resistance, which is multi-genic and not race specific (Black, 1970), has been found in S. tuberosum (Ross, 1986; Wastie, 1991), and a number of other Solanum species (Cañizares and Forbes, 1995; Colon et al., 1995a; Colon et al., 1995b; Landeo et al., 1995). It has also been found in S. demissum that possessed R genes (Glendinning, 1983). Several components of field resistance in potatoes have been identified that affect the pathogen's infection efficiency, lesion growth rate, generation time, sporulation capacity and sporulation period (Colon et al., 1995a; Birhman and Singh, 1995). The relative importance of these individual components may vary among Solanum species (Colon et al., 1995a) and environmental conditions can influence the expression of field resistance (Umaerus and Umaerus, 1994).

Several European cultivars were reported to have good levels of field resistance to late blight (Joosten, 1991). The Polish cultivars Bzura and Stobrawa were reportedly highly resistant to foliar late blight, but not as resistant to tuber late blight (Joosten, 1991). The cultivar Libertas from the Netherlands was reportedly resistant to both foliar and tuber late blight (Joosten, 1991). The American cultivars Elba (Thurston et al., 1985) and Krantz (Lauer et al., 1988) were reported to have some tolerance to late blight. A number of breeding selections from the USDA programs in Beltsville, Maryland (B numbered selections) (Goth and Haynes, 1997) and, Aberdeen, Idaho (A numbered selections) (J. Pavek, personal communication) have also been reported to have some resistance to late blight.

With the emergence of new genotypes of the fungus, and with the potential for genetic recombination between A1 and A2 mating types, information on the effect of pathogen x host x environment interactions on the phenotypic expression of stability of resistance to late blight in potatoes will become extremely important. Inglis et al. (1996) found that potato cultivar rankings in response to infection by the US-6 genotype of P. infestans were nearly identical to rankings obtained in previous years with the US-1 isolates. However, Sujkowski et al. (1996) indicated that the Polish cultivar Bronka had high levels of resistance to the old European genotypes of P. infestans, but had lower resistance to the new European populations.

Several excellent review articles on phenotypic stability are available (Freeman, 1973; Lin et al., 1986; Becker and Léon, 1988). One of the assumptions underlying the analysis of genotype x environment interactions in parametric analysis is homoscedasticity, that is, that error variances are constant over all locations (Neter and Wasserman, 1974), an assumption that can be tested (Bartlett, 1937).

Nonparametric measures of phenotypic stability involving the variance or standard deviation of the ranks of a genotype in different environments have been used by several researchers (Thomson and Cunningham, 1979; Léon and Becker, 1988). These nonparametric measures of phenotypic stability do not depend on any assumptions about the distribution of phenotypic observations (Huehn, 1990). Huehn has proposed adjusting measured observations on a genotype for their genotypic effects (1990) and for his adjusted values he has discussed the approximate tests of significance developed by Nassar and Hühn (1987). Lu (1995) has written a program in the SAS language for personal computers to estimate Huehn's nonparametric stability statistics, thus facilitating the calculation and use of these statistics.

Considering the evidence of recent immigrations of new genotypes of P. infestans, the durability of resistance is of paramount concern to breeding programs. The purposes of this study were to determine 1) the levels of resistance present in sixteen potato clones that reportedly had some resistance to P. infestans and, 2) the phenotypic stability of this resistance across environments in the United States in 1996.

MATERIALS AND METHODS

Sixteen potato clones reportedly resistant to late blight were successfully established in tissue culture during 1995. These cultures were tested for potato viruses A, X, Y, M, S, and leafroll using ELISA, and potato spindle tuber viroid

using cDNA techniques by Agdia (Agdia, Inc., Elkhart, IN). None of the viruses nor the viroid was detected, with the exception that most clones were infected with PVS. Plantlets were micropropagated and approximately 200 plantlets of each clone were transplanted into Jiffy Mix (Jiffy Products of America, Inc., West Chicago, IL) in the greenhouses at Beltsville, MD during the fall of 1995. In early December, minitubers were harvested from these plants. A minimum of fifteen minitubers of each of the sixteen clones were distributed to cooperating scientists in eight locations across the US for planting and evaluation. A listing of the locations, soil type at the location, the planting date, and evaluation dates for late blight is given in Table 1.

Minitubers were planted in a randomized complete block design consisting of three replications of five hills per clone at all sites except for New York, where four replications of five hills per clone were planted, and North Dakota, where minitubers were planted in a completely randomized design consisting of three plots of five hills per clone. Every other row or every third row in the field, depending on location, was planted with Russet Burbank to be used as a late blight spreader row, except for Florida, where Red LaSoda was planted in place of Russet Burbank. All locations inoculated the plots with US-8 strains of *P. infestans* (A2 mating type, metalaxyl-resistant) [Goodwin *et al.*, 1995a] except for Maine and Wisconsin, which relied on natural infestations for late blight.

Plants were evaluated for late blight at approximately weekly intervals during the growing season. Late blight readings were recorded on a plot basis as either the percent foliage infected or by the Horsfall-Barratt scale (1945). Hors-

fall-Barratt ratings were converted to mean percentage values by using the mid-point value in each interval for further analysis. Area under the disease progress curve (AUDPC) was calculated (Shaner and Finney, 1977) using data from weekly evaluations until at least two plots at that location were 100% infected. AUDPC was subjected to standard analysis of variance using proc glm (general linear model) in SAS (1987) by location. Heterogeneity of variance was tested using Bartlett's test (Bartlett, 1937).

Mean AUDPC was calculated for each clone at each location. Clones were then ranked on mean AUDPC from lowest to highest within locations. These rankings were analyzed for the nonparametric measures of phenotypic stability developed by Huehn (1990): mean absolute rank difference and variance of the ranks. The PC-SAS program developed by Lu (1995) was utilized for these analyses.

RESULTS AND DISCUSSION

Area under the disease progress curve was analyzed separately for each location. There were significant differences among clones for AUDPC at each location (Table 2). No emergence problems were reported at any of the locations. Bartlett's test (Bartlett, 1937) indicated that heterogeneity of variance among locations was significant (χ^2=92.3, P<0.01). Therefore, data were not combined across locations for further parametric analyses. The variances ranged from a low of 6,239 at NY to a high of 223009 at MI. The coefficient of variation ranged from a low of 14 in ME to a high of 56 in MI. The late blight infestation in MI was very erratic, and this is reflected in the high variance and coefficient of variation observed at this site. A more uniform distribution of the late blight infestation was observed at the other seven locations.

A listing of the sixteen clones, their mean AUDPC rating and the ranking within locations is given in Table 3. Mean AUDPC ranged from a low of 280 in PA to a high of 867 in ME. FL was generally cool, but dry, and supplied irrigation during the growing season. MI irrigated in August when conditions became dry. ME had no irrigation ability and mid-August to mid-September was on the dry side, but cool. MN had below average rainfall and above average temperatures; irrigation was supplied every third morning after inoculation. ND had no irrigation ability and was fairly cool and dry prior to mid-August; temperatures became warmer after mid-August and on 1 September 5.7 cm of rain fell. NY irrigated 5 evenings a week (0.25 cm. per evening) after mid-August. The weather in PA was cool and wet all season and they did not have to irrigate. WI irrigated three times weekly up to 5.3 cm

TABLE 1.—*Locations of the late blight trials in 1996, soil type, date plots were planted, and dates plots were evaluated for late blight.*

Location	Soil Type	Planting Date	Evaluation Dates
Hastings, FL	Wabasso sand	February 20	4/19, 4/23, 4/28, 5/2
East Lansing, MI	sandy loam	May 28	8/9, 8/12, 8/20, 8/26, 8/30, 9/13, 9/20
Presque Isle, ME	gravelly loam	May 24	8/8, 8/14, 8/21, 8/28, 9/4
Rosemount, MN	silt loam	May 30	8/15, 8/22, 8/29, 9/11
Prosper, ND	clay loam	June 3	8/9, 8/17, 8/20, 8/30, 9/6
Freeville, NY	gravelly loam	June 26	8/22, 8/30, 9/2, 9/4, 9/6
Rock Springs, PA	silty clay loam	June 3	8/20, 8/26, 8/30
Hancock, WI	Plainfield loamy sand	May 1	7/22, 7/29, 8/5, 8/12, 8/19

TABLE 2.—*Analysis of variance on area under the disease progress curve (AUDPC) and the coefficient of variation by location for 16 potato clones evaluated for late blight resistance in the US during 1996.*

Source	Type III Mean Squares							
	FL	MI	ME	PA	NY	MN	WI	ND
Rep	157904**	4179483**	46501*	7921	7175	45679	978555**	na [a]
Clone	85621**	1106375**	353211**	120927**	175751**	626676**	459690**	202465**
Error	8578	223009	14056	10597	6239	26975	60210	33075
Coefficient of variation	28	56	14	37	22	31	42	28

[a] North Dakota planted using a completely randomized design.
*,** Significant at the 5% and 1% levels, respectively.

per week; June and July were abnormally cool and wet while August and September were dry and warm. Thus, the fungal pathogen was exposed to a wide range of growing environments during the season.

The four potato clones with the lowest mean AUDPC were all from U.S. potato breeding programs: AWN86514-2, B0692-4, B0718-3 and B0767-2 (Table 3; Figure 1). The European potato clones with the lowest mean AUDPC were Bzura, Greta, Libertas and Bertita. Both of the North American cultivars, Elba and Krantz, were ranked in the lower half among the sixteen clones tested. However, even the clones ranked in the lower half had some tolerance to late blight as compared to the Russet Burbank/Red LaSoda spreader rows. The progression of late blight in the Russet Burbank uninoculated spreader rows was recorded in ME and WI. The mean area under the disease progress curve for Russet Burbank was 1363 and 1812 in ME and WI, respectively.

Two nonparametric statistics developed by Huehn (1990) are independent of the genotypic value, namely, $S^{(1)}_i$, which measures the mean absolute rank differences of a clone over all locations, and, $S^{(2)}_i$, which measures the common variance of the ranks. Neither of these statistics was sig-

TABLE 3.—*Mean area under the disease progress curve (AUDPC) for each of 16 potato clones evaluated at eight sites across the United States in 1996 and the rankings of AUDPC (RANK) within sites.*

| CLONE	FL		MI		ME		MN		ND		NY		PA		WI	
	AUDPC	RANK	AUDPC	RANK	AUDPC	RANK	AUDPC	RANK	AUDPC	RANK	AUDPC	RANK	AUDPC	RANK	AUDPC	RANK
A84118-3	284	7	1113	11	1053	11	997	14	612	8	590	14	484	12	800	11
AO80432-1	254	6	690	9	1112	13	832	13	761	12	518	12	555	15	1153	14
AO84275-3	395	10	1089	10	1090	12	387	8	633	9	296	7	347	11	850	12
AWN86514-2	136	3	296	3	374	3	44	1	377	3	101	3	46	2	41	1
B0692-4	87	1	653	8	412	4	73	3	334	2	70	2	26	1	141	3
B0718-3	130	2	126	1	329	2	72	2	444	4	167	4	61	3	211	4
B0749-2F	571	15	1212	12	1323	16	601	10	908	13	579	13	498	13	491	8
B0767-2	141	4	191	2	258	1	93	4	327	1	64	1	79	4	71	2
Bertita	309	8	649	7	929	7	325	6	648	10	302	9	290	10	565	9
Bzura	320	9	300	4	713	5	155	5	554	6	242	5	123	5	247	5
CO083008-1	413	11	1809	15	1117	14	1387	15	1080	15	662	15	546	14	1163	15
Elba	485	13	1269	13	1037	10	436	9	968	14	464	11	215	7	878	13
Greta	195	5	399	5	957	8	384	7	493	5	270	6	124	6	481	7
Krantz	552	14	2374	16	1256	15	1526	16	1158	16	708	16	597	16	1186	16
Libertas	474	12	531	6	876	6	629	12	593	7	302	8	224	8	378	6
Stobrawa	586	16	1294	14	1027	9	613	11	693	11	405	10	270	9	659	10
LSD (.05)	154		789		198		274		303		112		172		409	
Mean	333		843		867		533		656		359		280		582	
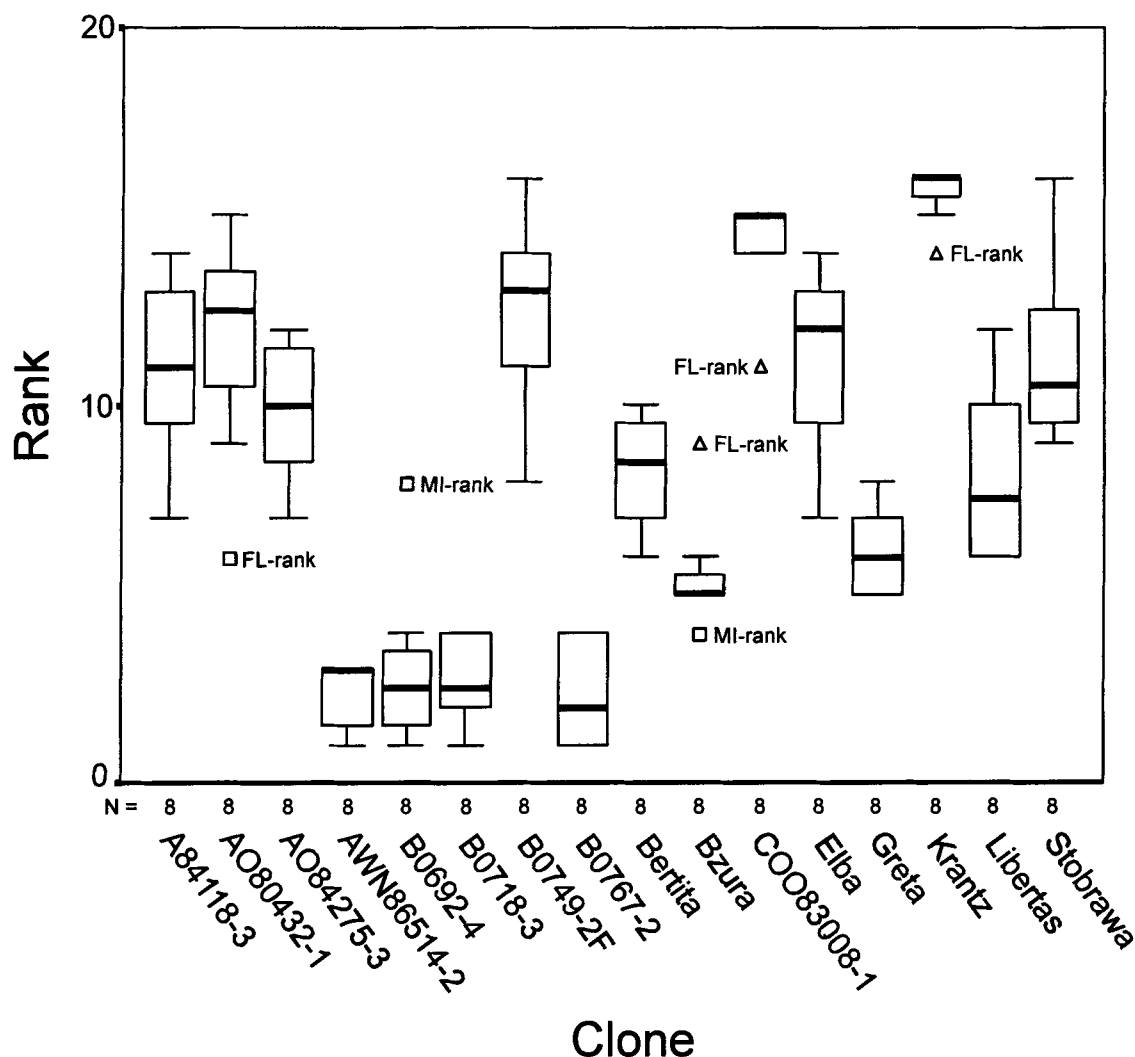
FIGURE 1

Box and whisker plot of rank for mean area under disease progress curve (AUDPC) of sixteen clones evaluated at eight locations in the late blight study. For each clone, the box represents the interquartile range, the heavy horizontal line represents the median, and the fine horizontal lines represent the minimum and maximum values excluding outliers and extreme values. The squares designate outliers (values that are 1.5-3.0 box lengths from the upper or lower edge of the box) and the triangles designate extreme values (> 3.0 box lengths from the upper or lower edge of the box).

nificant, indicating that the clonal performance, as measured by the ranking on mean AUDPC, was phenotypically stable across environments (i.e., no genotype x environment interaction on the ranking of the clones was detected) (Table 4). During 1996, all of the plots were either inoculated with US-8 strains of *P. infestans* or US-8 strains were identified in naturally infested plots. With the US-8 genotype common to all locations and a common seed source supplied to all locations for evaluation, it could be argued that genotype x environment interactions would not be expected. However, environment does play a role in the development of late blight

(Umaerus and Umaerus, 1994) and the growing conditions for both the pathogen and the potato genotypes at the eight locations were different in terms of daily temperature fluctuations, rainfall, soil types, planting dates, inoculation dates, potato seed age, etc. Genotype x environment interactions could still be important if the variable analyzed was actually AUDPC instead of the rankings of mean AUDPC. However, in view of the difficulty in standardizing the testing from one location to the next and the heterogeneity in variances, the statistical assumptions necessary to analyze AUDPC by parametric methods were not met. Nonparametric analyses elim-

TABLE 4.—*Mean area under disease progress curve*
(MAUDPC), mean of the absolute rank
differences of a clone ($S^{(1)}_i$), rankings of the
clones from lowest MAUDPC to highest (rank)
and its approximate test of significance ($Z^{(1)}_i$),
and, common variance of the ranks ($S^{(2)}_i$) and
its approximate test of significance ($Z^{(2)}_i$)
across locations.[1]

Clone	MAUDPC	Rank	$S^{(1)}_i$	$Z^{(1)}_i$	$S^{(2)}_i$	$Z^{(2)}_i$
A84118-3	741.63	13	4.82	0.22	16.70	0.34
AO80432-1	734.38	12	6.21	0.73	26.57	0.47
AO84275-3	635.88	9	6.20	0.70	28.53	0.87
AWN86514-2	176.88	2	5.71	0.15	23.64	0.09
B0692-4	224.50	4	3.11	4.37	7.13	3.28
B0718-3	192.50	3	6.64	1.59	30.57	1.43
B0749-2F	772.88	14	5.07	0.05	19.14	0.07
B0767-2	153.00	1	5.79	0.20	23.07	0.05
Bertita	502.13	8	3.57	2.73	9.43	2.30
Bzura	331.75	5	6.04	0.47	26.55	0.46
COO83008-1	1022.13	15	7.11	2.90	38.84	5.09
Elba	719.00	11	6.57	1.43	29.71	1.18
Greta	412.88	6	4.59	0.47	14.71	0.70
Krantz	1169.63	16	7.04	2.67	42.84	7.67
Libertas	500.88	7	4.50	0.59	14.00	0.87
Stobrawa	693.38	10	4.36	0.82	13.64	0.95
Sum				20.09		25.85

[1]The Z-statistics are measures of stability. The tests for the significance of the sum of $Z^{(1)}_i$ or $Z^{(2)}_i$ are compared to a χ^2 value of 26.30. Individual $Z^{(1)}_i$ or $Z^{(2)}_i$ are compared to a X^2 value of 8.73.

inated the difficulties encountered by slight variations in experimental design, variations in the time intervals between late blight evaluations, and the variation between locations.

The information developed here serves several useful purposes. First, it identifies germplasm that has some resistance to the US-8 genotype of *P. infestans* for potato breeders to use as parental material in hybridization programs. Second, under the conditions in which this research was conducted, genotype x environment interactions on the rankings of mean AUDPC for these clones were not important. With only one year of testing, these results are tentative. However, the eight locations in which these clonal materials were tested did represent a wide range of environments across the United States. Testing in additional years is needed to expose these clones to attack by a variety of different *P. infestans* genotypes before final conclusions can be made. In future efforts it will be important to introduce variability of *P. infestans* genotypes to stability analysis. This study argues, however, that interactions of genotype x environment are not

predominant in late blight breeding. Third, it has brought together a network of researchers for a National Late Blight Resistance Trial who are committed to evaluating the potential impact of genotype x environment interactions on resistance to late blight in potatoes. Hopefully, this will serve as a model for other researchers involved in collaborative projects of this magnitude. Fourth, it has identified and demonstrated the usefulness of nonparametric statistics for the evaluation of data of the type collected in this study where variation among the environmental locations, and variations among the hosts and pathogens are present.

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